RESPONSES OF BATS FROM TEMPERATE REGIONS TO CHANGES IN AMBIENT TEMPERATURE

WAYNE H. DAVIS AND OLA B. REITE[1]

Department of Zoology and Department of Physiology & Biophysics, University of Kentucky, Lexington, Kentucky 40506

Although bats in temperate regions are usually thought to migrate to warmer climates or to retreat underground beyond the frost line for the winter, many species commonly encounter freezing temperatures. Big brown bats (*Eptesicus fuscus*) winter in buildings in areas where the outdoor temperature may drop to below −30° C. (Nero, 1959). This bat appears in numbers in caves only during very cold weather, and individuals move to and from their hibernating sites throughout the winter (Mumford, 1958). Pipistrels (*Pipistrellus subflavus*), Indiana bats (*Myotis sodalis*) and little brown bats (*Myotis lucifugus*) all hibernate in caves. The pipistrel is a hardy bat whose numbers present at the place used for hibernation depend upon the severity of the weather (Davis, 1959). Indiana bats enter the caves in mid-autumn, and occasionally die of cold when hibernating too near the entrance. The little brown bat enters hibernation in early autumn, and some individuals retreat into crevices, apparently in response to cold weather. A few bats of this species also succumb to cold during hibernation (Davis and Hitchcock, 1965). The red bat (*Lasiurus borealis*) is a tree-dwelling species which winters in regions where temperatures frequently stay well below freezing for days (Davis and Lidicker, 1956).

As ambient temperature drops below 0° C. a hibernating bat may respond in one of three ways. It may increase its body temperature and arouse from hibernation; it may remain in hibernation and maintain its body temperature by increasing the metabolism sufficiently to compensate for increased heat loss; or it may remain passive during cooling and eventually freeze. Maintenance of a relatively stable body temperature by metabolic compensation has been reported for *Lasiurus borealis* and *Myotis lucifugus* (Reite and Davis, 1966).

The present investigation was undertaken to relate the known differences in the ecology of the five species of bats mentioned above to possible differences in their response to changes in ambient temperature.

Materials and Methods

Experimental animals (Table I) were captured in Kentucky. All were obtained from buildings or caves except the red bats, which were netted near certain cave entrances where they regularly appear in late summer and early fall. Upon arrival at the laboratory, the bats were placed in a temperature-controlled room and kept

[1] International Postdoctoral Research Fellow, U. S. Public Health Service (Award No. 1 F05-TW-687-01). Present address: Institute for Experimental Medical Research, Ullevaal Hospital, Oslo, Norway.

overnight at 5° C. Some were restrained by taping the wings to a wooden block, and a copper-constantan thermocouple connected to a Brown electronic potentiometer was inserted into each bat's rectum. Other bats were left unrestrained with rectal thermocouples taped in place, and still others without any recording device were put into individual jars covered with a screen. The next morning temperature was lowered or increased stepwise by units of 2–10° C. Ambient and rectal temperatures were recorded continuously, and the bats were observed for signs of activity. Electrocardiograms were taken on two or more individuals of each species. The leads were fastened to the skin of the bats with alligator clips, and the signals recorded with a Sanborn amplifier and recording system.

Results

Ambient temperature of 5° C.

After staying overnight in the room with the temperature control set at 5° C., all specimens appeared to be dormant except for *P. subflavus* and *E. fuscus,* of which species single bats were occasionally found to arouse spontaneously and re-enter the dormant state even when undisturbed. Most unrestrained bats suspended themselves by their feet from the screen covering the jars. *L. borealis* brought the large furred interfemoral membrane up over the body, covering the wings, except at the wrists, and all the ventral surface up to the chin (Fig. 1).

Table I

Experimental animals

Species	Number		Dates of collection	Body weights (g.)
	Males	Females		
L. borealis	8	2	Sept.–Oct.	9–13
M. lucifugus	15	10	Sept.–Dec.	7–10
M. sodalis	8	9	Oct.–Dec.	8–10
E. fuscus	8	8	Sept.	19–25
P. subflavus	19	6	Oct.–Dec.	5–6

Rectal temperatures of dormant bats at 5° C. were always less than one degree above ambient. Heart rates varied considerably among species (Table II). Spontaneous and rapid changes in heart rate, not accompanied by noticeable changes in conditions of torpor or rectal temperature, were noted in *E. fuscus* and *P. subflavus.*

Increasing temperature

Stepwise increase in ambient temperature could be performed up to about 10° C. without any change in the appearance of the bats. All seemed to remain dormant. When ambient temperature was changed from 10° C. to 15° C., arousal began in all species except *L. borealis.* In one series of experiments which included 8–12 unrestrained individuals of each of *E. fuscus, P. subflavus, M. lucifugus* and *M. sodalis,* 3–4 bats of each species were active within 60–80 minutes of the increase

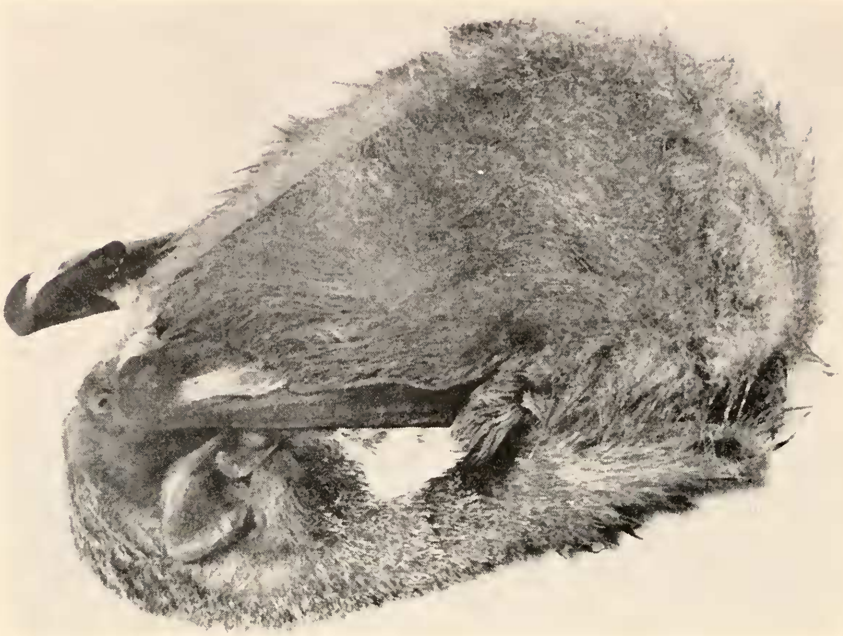

FIGURE 1. Male red bat, *L. borealis,* in dormancy at 5° C.

in temperature. In experiments with *L. borealis* there were no signs of arousal at 15° C. In two individuals of this species taken to higher temperatures, arousal was induced at about 20° C.

During passive warming to 10° C., rectal temperatures remained within 1° C. above ambient. Bats which began to arouse after ambient temperature was raised to 15° C. showed an increase in rectal temperature. In *E. fuscus* the temperature reached 35–38° C. in 1–2 hours.

Heart rates after passive warming of *M. lucifugus*, *E. fuscus*, and *L. borealis* to 10° C. are given in Table II. Arousal from the dormant state was always accompanied by a rapid increase in heart rate.

TABLE II

Heart rates in dormant bats. Counts were made over several 30–60-sec. periods chosen at random from 6–8 recordings each lasting 5–10 min. and taken at intervals of at least 1 hour

	Ambient temperature (° C.)	Heart rate (beats/min.)
L. borealis	5	10–16
L. borealis	10	16–22
M. lucifugus	5	24–32
M. lucifugus	10	44–56
E. fuscus	5	42–62
E. fuscus	10	64–88
M. sodalis	5	36–62
P. subflavus	5	24–80

Decreasing temperature

Striking differences among species were evident in response to decreasing ambient temperature to 0° C. and below. *E. fuscus* invariably aroused from dormancy and became active within 40–120 minutes. Both restrained and unrestrained individuals were able to remain active for several hours, even at an ambient temperature as low as −5° C. Attempts to make them re-enter dormancy by keeping them overnight at −3° C. to −5° C. were unsuccessful, but this could easily be achieved by changing ambient temperature to 5° C. About half the *P. subflavus* studied aroused following a temperature change from 5° C. to 0° C. None aroused when the temperature was lowered from 5° C. to −5° C. in one step. *M. lucifugus* remained dormant when ambient temperature was lowered to 0° C. Further lowering to −5° C. induced arousal in a few, whereas an abrupt change from 5° C. to −5° C. induced arousal in all bats of this species. *M. sodalis* responded similarly. *L. borealis* remained dormant both during stepwise and abrupt lowering of ambient temperature from 5° C. to −5° C. Abrupt exposure of *L. borealis* to subfreezing temperatures induced an almost instantaneous increase in the rate and depth of respiration.

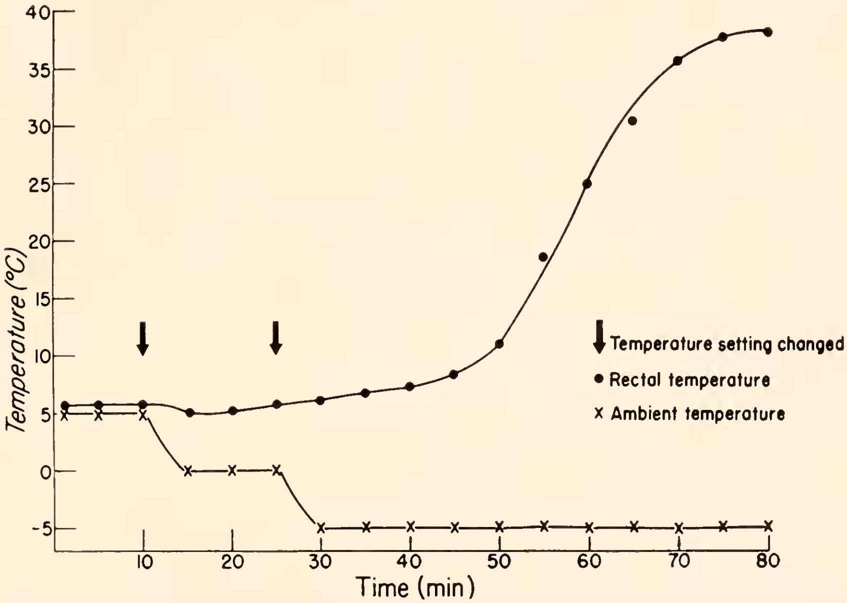

FIGURE 2. Changes in rectal temperature of *E. fuscus* during arousal from dormancy in response to lowering of ambient temperature.

Following a change of ambient temperature from 5° C. to between 0° C. and −5° C., dormant *E. fuscus* showed a slight decrease in rectal temperature followed within about 30 minutes by a rapid increase (Fig. 2). The increase in rectal temperature was accompanied by increasing heart rate. As reported previously (Reite and Davis, 1966), *L. borealis* and *M. lucifugus* show an increase in the difference between rectal and ambient temperature and an increased heart rate when ambient temperature is gradually decreased. A similar response was found in *M. sodalis.*

P. subflavus, tested for response to an abrupt lowering of ambient temperature, showed low rectal temperature even after more than one hour at −5° C. A comparison between unrestrained *P. subflavus* (5 individuals) and *M. lucifugus* (7 individuals) by exposing them to a temperature change from 5° C. to −5° C. revealed a marked difference in their responses. After one hour the rectal temperatures of *P. subflavus* ranged from −1.5° C. to 0° C. Four of the *M. lucifugus* were fully active with rectal temperature ranging from 34° C. to 39° C., and the other three were in various stages of arousal (rectal temperatures 5–14° C.). *P. subflavus* kept at −5° C. for 3–4 hours died.

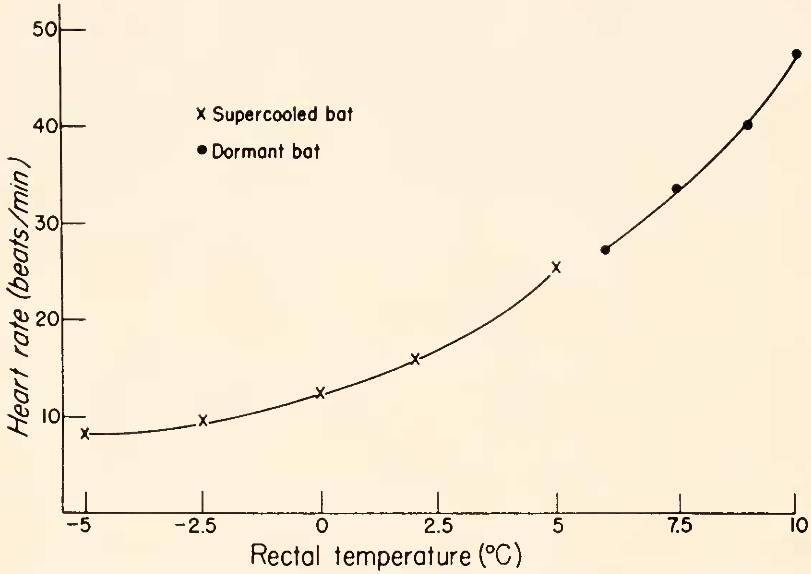

FIGURE 3. Changes in heart rate in *M. lucifugus* during passive warming of a supercooled individual from −5° C. to 5° C. and a dormant one from 5° C. to 10° C.

Supercooling and freezing

Rectal temperatures of restrained dormant *M. lucifugus, M. sodalis* and *L. borealis* kept at −5° C. stayed 1–4° C. above ambient for 2–3 hours, the central body temperature being probably still higher than that of the rectum. During this time, the bats continued breathing and maintained increased heart rate. When kept at −5° C. for longer periods the breathing ceased and rectal temperature dropped to ambient, indicating that the temperature gradients between central parts of the body and the periphery were disappearing. Only bats in this latter condition will be termed supercooled, although local tissue temperatures in bats of the former category were also well below the freezing point of tissue fluids. Spontaneous tissue freezing followed by death occurred in some of the supercooled bats. Whether or not freezing occurred was determined by inspection. In those bats which did not freeze, heart beats continued and rectal temperature remained constant at −5° C. Several bats of each species were removed from the cold room and exposed to room temperatures after having been kept in the supercooled state with ceased breathing for 5–8 hours, while others in the same condition were left in the cold room, where the temperature was then changed to 5° C. We tested all bats for ability to respond to stimuli by forceably opening the eyes and mouth, extending the wings, and probing the bodies with fingers. Unlike the situation during dormancy, the bats lacked muscle tone and did not respond to stimuli. After 8–16 minutes at an ambient temperature of 24° C. the bats which had been removed from the cold room began slight movements of the feet and soon resumed breathing. Within 30–45 minutes they had recovered completely and were capable of normal flight. They were kept overnight in the laboratory, tested again for normal flight, and released in apparently good condition. In the supercooled bats left in the cold room at 5° C., heart rate increased slowly during rewarming (Fig. 3), breathing was resumed, and these bats also recovered completely.

No attempt was made to test survival time of supercooled bats which had ceased breathing. We succeeded in keeping one individual of *M. lucifugus* supercooled at −6.5° C. for half an hour and rewarming it without ice formation. This bat also survived. Occasionally, during exposure to sub-zero temperatures, freezing occurred in peripheral tissues of bats which had not become supercooled. These animals recovered if removed from the cold room before ice formation had taken place in more central parts of the body. However, when spontaneous freezing occurred in already supercooled animals it seemed inevitably to be lethal. Freezing in supercooled bats was accompanied by a rapid rise in body temperature to a level between −0.5° C. and −1° C., and the process could be induced by pricking with a needle. Supercooling to below −5° C. for any length of time seemed difficult, as further lowering of the temperature greatly enhanced the tendency to spontaneous ice formation.

Discussion

Since Eisentraut (1934) published one of the first accounts on the different physiological states of bats with respect to ambient temperature, numerous reports have followed. The literature is covered in a recent review (Stones and Wiebers, 1965).

Hibernating bats have different ways of surviving when ambient temperatures drop below freezing. According to our experiments, *E. fuscus* will awaken, a reaction which also seems to be normal in other hibernators (Hock, 1960). During extremely cold weather it is not unusual for bats of this species to be seen in flight in buildings. Common speculation among students of Chiroptera is that overheating of the hibernating sites by the heating systems of the buildings is the likely cause of arousal. From the present results we believe it is more probable that the hibernating sites become too cold, which causes the bats to move to warmer places. This assumption is supported by the observation that *E. fuscus* undergoes considerable intercave movement at air temperatures below freezing (Mumford, 1958).

L. borealis responds to freezing temperatures by increasing its metabolism enough to maintain its body temperature above a dangerous lower limit (Reite and Davis, 1966). These animals do not hibernate in caves, and it would be to their disadvantage to arouse, since arousal would use far more energy than regulation during dormancy. Red bats also remain dormant when ambient temperature rises. Our observations indicate that whereas other species will arouse at temperatures between 10° C. and 15° C., red bats remain in dormancy up to a temperature of about 20° C. unless handled or otherwise disturbed. This is an important adaptation. These animals are exposed to wide fluctuations in temperature in their natural environment, and cannot afford to become active until it is warm enough to obtain enough food to compensate for loss of stored energy. Thus in winter they do not fly unless it is warm enough for insect flight. Davis and Lidicker (1956) found that red bats became active only on days when temperatures rose to 19° C. or above. Constantine (1958) observed the closely related *L. seminolus* hibernating in their natural environment, and reported that they awoke and flew only when environmental temperatures reached 21° C. Both reports give support to the present findings. *L. borealis* joins other species of bats in swarming at the caves in early fall (Davis, 1964), but never hibernates there. Occasionally, red bats enter rooms in certain caves, cannot find their way out again, so hang up and become dormant. Such bats invariably perish (Myers, 1960), perhaps being unable to arouse spontaneously at cave temperatures. Thus red bats seem to be so adapted to survival outside that they are unable to survive in caves.

The anatomical structure and the behavior of *L. borealis* are better modified for survival at low temperatures than those of any of the other species studied. Except for the ears and parts of the wings, this bat is completely furred. The furred interfemoral membrane and the long tail, in relation to body length, is probably of significance in heat conservation during hibernation when the bat uses the interfemoral membrane to cover the ventral surface (Fig. 1). The short rounded ears may also enable this bat to tolerate exposure to cold better than the other species.

The only bat in which the response was not what might be expected from previous knowledge of its behavior in its natural environment was *P. subflavus*. Since bats of this species move into the caves in numbers only after periods of freezing weather, we would expect them to arouse as temperatures approach and go below freezing. However, our experiments showed that they aroused only in response to moderate lowering of ambient temperature. The reason may be that their small size does not allow them to generate enough heat to exceed the heat loss when ambient temperature is lowered abruptly to −5° C. Even in larger bats the increase in body temperature is slow during the initial steps of arousal. The low tolerance of *P. subflavus* to supercooling makes it reasonable to believe that their natural way of responding is to come out of hibernation. They may survive outside the caves during early moderate cold periods and arouse and move into the caves when the most severe part of the winter is approaching. Folk (1940) has suggested that the first cold periods of winter may indicate to bats the suitability of their resting place for hibernation.

Both Kayser (1940) and Hock (1951) noted increased respiratory exchange in dormant bats exposed to temperatures near 0° C. The justification for considering this as a true thermoregulatory response is supported by the present observations in bats of the species *L. borealis, M. lucifugus* and *M. sodalis,* which established an increased difference between rectal and ambient temperature when the latter was decreased.

If taken as an indicator of metabolism, the heart rate in dormant bats at 5° C. should reflect the relative efficiency or depth of hibernation in the different species. Of the species studied, *L. borealis* may be considered best adapted for hibernation. Those with the highest heart rates (*E. fuscus, M. sodalis* and *P. subflavus*) should be more prone to arousal. This assumption is supported by the finding of spontaneous rapid changes in the heart rate of dormant *E. fuscus* and *P. subflavus,* and also by the observation that individuals from these species occasionally became active and re-entered dormancy even when kept at a stable ambient temperature of 5° C. *M. lucifugus* is intermediate. Whether this bat will respond to a lowering of ambient temperature by increasing its metabolism enough to compensate for increased heat loss (thermoregulation) or by arousal from dormancy, seems to depend on the abruptness and severity of the cold exposure. Seasonal differences may also be present. The heart rate of *M. lucifugus* in dormancy at 5° C. is in the same range as that reported by Johansen and Krog (1959) for the birchmouse, a hibernator of comparable size.

Cooling of bats to about −5° C. without formation of ice in the body is in agreement with previously obtained results (Kalabuchow, 1935). The slow increase in heart rate in supercooled *M. lucifugus* during rewarming from −5° C. to 5° C. (Fig. 3) corresponds fairly well to the rate change found in isolated hearts of this species over that part of the same temperature range where such studies have been performed (Michael and Menaker, 1963). The heart rate in dormant *M. lucifugus* at temperatures of 5–10° C. is also in the same range as that of the isolated heart. These observations suggest that in supercooled bats with ceased breathing and in dormant bats at neutral ambient temperatures (5–10° C.) the heart is not under any neural influence. This is different from the situation in dormant bats of *L. borealis* and *M. lucifugus* exposed to stepwise lowering of ambient temperature from 5° C. In these bats the heart rate increases with decreasing temperature (Reite and Davis, 1966).

Supercooling of bats could be of significance for survival during short term exposure to sub-zero temperatures, a situation which may occur following a change of wind direction at the entrance to a cave used for hibernation. However, supercooling is an unstable condition and must be transient.

We wish to thank Roger W. Barbour for photographing the dormant red bat, and Loren D. Carlson, Eugene C. Crawford and Marion D. Hassell for reading the manuscript.

Summary

1. Responses to upward and downward changes in ambient temperature from 5° C. were studied in dormant bats of the species *E. fuscus, P. subflavus, M. sodalis, M. lucifugus* and *L. borealis.* Rectal temperatures and heart rates were recorded.

2. Except for *L. borealis* which did not arouse until ambient temperature reached about 20° C., all species responded by arousal from dormancy when the temperature was increased to 15° C.

3. The effects of decreasing ambient temperature varied considerably among species. *E. fuscus* invariably aroused from dormancy. *L. borealis* never aroused but showed a thermoregulatory response by increasing its metabolism to compensate

for the increase in heat loss. The responses of the other species depended upon the abruptness of the temperature change. Abrupt lowering of ambient temperature tended to induce arousal in *M. lucifugus* and *M. sodalis*, whereas these species responded similarly to *L. borealis* when exposed to gradually decreasing temperature. *P. subflavus* usually aroused in response to a gradual decrease in ambient temperature, but seemed unable to arouse in response to abrupt lowering of temperature.

4. Bats of the species *L. borealis*, *M. lucifugus* and *M. sodalis* supercooled to −5° C. showed cessation of breathing, but slow heart beats continued for several hours. Passive rewarming was necessary for survival.

5. Many of the known differences in the ecology of the studied species of bats are reflected as differences in their response to changes in ambient temperature in the laboratory.

LITERATURE CITED

Constantine, D. G., 1958. Ecological observations on lasiurine bats in Georgia. *J. Mammal.*, **39**: 64–70.

Davis, W. H., 1959. Disproportionate sex ratios in hibernating bats. *J. Mammal.*, **40**: 16–19.

Davis, W. H., 1964. Fall swarming of bats at Kentucky caves. *Bull. Natl. Speleolog. Soc.*, **26**: 82–83.

Davis, W. H., and H. B. Hitchcock, 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. *J. Mammal.*, **46**: 296–313.

Davis, W. H., and W. Z. Lidicker, Jr., 1956. Winter range of the red bat, *Lasiurus borealis*. *J. Mammal.*, **37**: 280–281.

Eisentraut, M., 1934. Der Winterschlaf der Fledermäuse mit besonderer Berücksichtigung der Wärmeregulation. *Z. Morphol. Ökol. Tiere*, **29**: 231–267.

Folk, G. E., Jr., 1940. Shift of population among hibernating bats. *J. Mammal.*, **21**: 306–315.

Hock, R. J., 1951. The metabolic rates and body temperatures of bats. *Biol. Bull.*, **101**: 289–299.

Hock, R. J., 1960. Seasonal variations in physiologic functions of arctic ground squirrels and black bears. *In:* Mammalian Hibernation. Ed. by C. P. Lyman & A. R. Dawe. *Bull. Mus. Comp. Zool.*, **124**: 155–169.

Johansen, K., and J. Krog, 1959. Diurnal body temperature variations and hibernation in the birchmouse, *Sicista betulina*. *Amer. J. Physiol.*, **196**: 1200–1204.

Kalabuchow, N. I., 1935. Anabiose bei Wirbeltieren und Insekten bei Temperaturen unter 0°. *Zool. Jahrb., Abt. allg. Zool. Physiol.*, **55**: 47–64.

Kayser, Ch., 1940. Les échanges respiratoires des hibernants à l'état de sommeil hivernal. *Ann. Physiol. Physicochim. Biol.*, **16**: 127–221.

Michael, C. R., and M. Menaker, 1963. The effect of temperature on the isolated heart of the bat, *Myotis lucifugus*. *J. Cell. Comp. Physiol.*, **62**: 355–358.

Mumford, R. E., 1958. Population turnover in wintering bats in Indiana. *J. Mammal.*, **39**: 253–261.

Myers, R. F., 1960. *Lasiurus* from Missouri caves. *J. Mammal.*, **41**: 114–117.

Nero, R. W., 1959. Winter records of bats in Saskatchewan. *Blue Jay*, **17**: 78.

Reite, O. B., and W. H. Davis, 1966. Thermoregulation in bats exposed to low ambient temperatures. *Proc. Soc. Exp. Biol. Med.*, **121**: 1212–1215.

Stones, R. C., and J. E. Wiebers, 1965. A review of temperature regulation in bats (Chiroptera). *Am. Midl. Naturalist*, **74**: 155–167.